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Feeding outside the Forest: The Importance of Crop Raiding and an Invasive Weed in the Diet of Gallery Forest Ring-Tailed Lemurs *(Lemur catta)* following a Cyclone at the Beza Mahafaly Special Reserve, Madagascar

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Key Words
Crop raiding · Ring-tailed lemurs · Cyclone · Nutrition

Abstract

In January 2005, a cyclone hit southern Madagascar, including the Beza Mahafaly Special Reserve, disrupting the flowering/fruiting cycle of *Tamarindus indica,* leaving *Lemur catta* without its major food resource during reproductive periods. We studied two adjacent groups of *L. catta* during the late gestation period, and both groups ventured outside the reserve to feed. The Red group (RG) fed daily on cultivated sweet potato *(Ipomoea batatas)* leaves in a nearby field, and both groups consumed leaves and stems of the invasive terrestrial flowering herb Mexican prickly poppy *(Argemone mexicana)*, growing outside the reserve. The Green group (GG) spent significantly more time feeding than did RG, and more time feeding inside the forest compared to outside. The members of RG spent half of their time feeding in the crops, and nearly half of their diet consisted of easy-to-process sweet potato leaves. Additionally, RG defended and restricted GG's access to the crop territory. Of the two non-forest foods, *A. mexicana* leaves were higher in protein and most minerals (P, Mg, K and Na, but not Ca) and lower in fiber than sweet potato leaves, but sweet potato leaves were preferred by RG. *L. catta* is a markedly flexible primate with respect to diet, and switches to fallback foods from outside the forest during periods of low food availability. In the highly seasonal and unpredictable climate of southern Madagascar, such behavioral adaptations are important to the survival of this species.

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Introduction

Madagascar's unpredictable environment is often affected by cyclones, droughts and severe storms, which impact lemur populations [Ganzhorn, 1995; Gould et al., 1999; Wright, 1999; Gould et al., 2003; Ratsimbazafy, 2006; Ratsisetraina, 2007]. The Beza Mahafaly Special Reserve (BMSR) was hit by Cyclone Ernest in January of 2005. Massive defoliation and tree falls occurred and resulted in an overall reduction in forest food availability for *Lemur catta* inhabiting the reserve, particularly during the following reproductive season, as indicated by monthly phenological data collected by reserve staff [Razanajafy and Raznadrainy, pers comm.]. This is already a difficult time of year as gestation and early lactation correspond with the dry season in southern Madagascar [Jolly, 1984; Sauther, 1992, 1998; Wright, 1999]. Additionally, *Tamarindus indica* fruit, considered to be the most important food resource for gallery forest-dwelling *L. catta* [Budnitz and Dainis, 1975; Sauther, 1992; Rasamimanana and Rafidinarivo, 1993; Sauther, 1998; Jolly et al., 2002; Yamashita, 2002; Mertl-Millhollen et al., 2003; Gould, 2006; Koyama et al., 2006; Simmen et al., 2006], was absent due to the effects of the cyclone. In this paper, we describe the response by two groups of ring-tailed lemurs inhabiting BMSR to the resource shortage caused by Cyclone Ernest.

Ring-tailed lemurs are opportunistic frugivore/folivores that exploit a variety of plant- and non-plant-based resources, at all levels of the forest, as they become annually and seasonally available [Rasamimanana and Rafidinarivo, 1993; Sauther, 1994, 1999; Sauther et al., 1999; Simmen et al., 2006]. Despite being flexible foragers, ring-tailed lemurs residing in gallery forests are highly dependent on young leaves or fruits from the tamarind tree, *T. indica*, which are produced asynchronously and are present throughout the year [Sauther, 1998; Mertl-Millhollen et al., 2003; Simmen et al., 2006]. In times of food scarcity, ring-tailed lemurs often temporarily increase their home range to secure scarce food resources [Sussman, 1991; Sauther, 1998; Jolly and Pride, 1999; Mertl-Millhollen et al., 2006], and at these times critical 'fall-back foods' that are not normally eaten may prove crucial [Soma, 2006]. Additionally, very poor quality foods such as desiccated leaves and dry tamarind pods may be incorporated into the diet during periods of food shortage [Sauther 1992, 1994, 1998; Gould et al., 1999].

Crop raiding is a common occurrence worldwide in areas where farming abuts primate habitat [Naughton-Treves et al., 1998; Chakravarthy and Thyagaraj, 2005; Hill, 2005; Estrada, 2006; Wang et al., 2006; Agetsuma, 2007; Linkie et al., 2007; Ymke et al., 2007]. Agricultural products tend to be particularly nutritious and abundant, and thus can be valuable for wild primates, even in the face of potential risks associated with obtaining crop foods [Forthman-Quick, 1986; Hill, 2005]. Threat from humans can be particularly high during crop raiding, as farmers want to protect their agricultural investments [Saj et al., 1999; Hill, 2000; Naughton-Treves and Salafski, 2004; Estrada, 2006]. However, crop-raiding primates may be exempt from human-induced harm in areas where people hold traditional taboos or cultural beliefs that serve to protect primates [Saj et al., 1999; Loudon et al., 2006]. In fact, Loudon et al. [2006] found that lemurs at BMSR were exempt from human harm, even when crop raiding, because of the local belief that lemurs were at one time human.

At BMSR, predation threat increases once lemurs move outside the forest [Sauther, 2002]. For example, Sauther [2002] noted in a year-long study that all encounters between ring-tailed lemurs and the Madagascar harrier hawk occurred in open terrain such as meadows or clearings, and not in the forest, as this raptor favors open environments where it can attack its prey from directly above. Ring-tailed lemurs are also far more vulnerable to feral dogs when in open areas [Gould, 1996; Sauther, 1998, 2002; Gould and Sauther, 2006]. Thus, consequences of crop raiding may include increased stress, and bodily injury or even death from predation and human interference [Saj et al., 1999; Wheatley et al., 1999; Hill, 2000; Chism, 2005; Lee and Priston, 2005]. These risks are expected to be higher in females who are gestating or lactating, because they may be weighed down by their pregnancy or clinging infant, and unable to escape quickly from danger [Cords, 2002; Miller, 2002; Pazol and Cords, 2005]. Furthermore, clinging ring-tailed lemur infants can fall off mothers fleeing from predators and may become prey items. However, because of increased caloric requirements, reproductive females may be more likely to seek out crop foods, despite increased risks.

The inclusion of crop foods is likely to increase foraging efficiency, since animals eating these foods do not have to travel between patches as they deplete their immediate food source. Since crop raiding allows individuals to meet their metabolic needs sooner, animals can rest more or engage in other activities [Brennan et al., 1985; Altmann and Muruthi, 1988].

In light of the above information and the fact that Cyclone Ernest markedly reduced the availability of tamarind fruit, the preferred food of ring-tailed lemurs at BMSR in 2005, we investigated the following questions in two adjacent groups of ring-tailed lemurs residing in BMSR 7 months after Cyclone Ernest affected this region:

(1) Did access to a local villager's crop enable the Red group (RG) to spend less time feeding, when compared to the Green group (GG), which did not have primary access to the crop?
(2) Is there a difference in the consumption rate of 'fallback' non-forest foods consumed by each group compared with food consumed inside the forest?
(3) Of the two food types consumed outside the forest, sweet potato leaves and the leaves of Mexican prickly poppy, do the sweet potato leaves contain a higher degree of nutrients, as has been suggested previously for crop foods consumed by primates?
(4) Since this study was conducted during late gestation period, and in a year in which a natural disaster occurred, was there a sex difference in consumption rates of the non-forest fallback foods?

Methods

Data Collection

The study took place at BMSR in southwestern Madagascar, 23°30′ South latitude and 44°40′ East longitude. Continuous time focal animal data [Altmann, 1974] were collected by M.L. throughout August and early September of 2005, a period corresponding to late gestation in *L. catta* at BMSR. Data were collected on all adults (n = 18) from two neighboring social groups (RG and GG) of ring-tailed lemurs at BMSR. RG contained 3 adult females and 4 adult males, and GG was comprised of 6 adult females and 5 adult males. Ten focal animal sessions, 15 min in duration, were collected for each focal animal. When an animal was feeding, M.L. noted the animal's location, amount eaten (number of leaves or bites), and the plant part ingested. The home ranges of both groups bordered the Sakamena River in the eastern part of the reserve. RG's home range also included a local villager's field, where both a cultivated crop

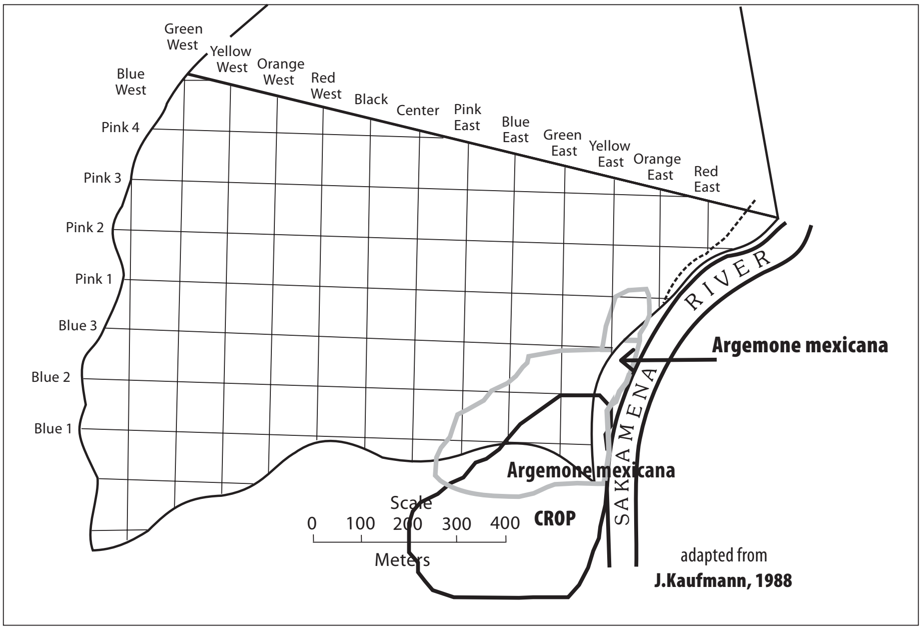

Fig. 1. Map of BMSR and home ranges of both study groups. RG's home range is depicted in black and GG's home range is in light grey. The location of the sweet potato crop and the patches of *A. mexicana* are labeled.

(Ipomoea batatas) and weeds *(Argemone mexicana)* grow and GG's home range included a portion of the dry riverbed, where *A. mexicana* grows (fig. 1).

After gaining permission from the villager who tended the cultivated field, M.L. collected representative samples of *I. batatas* leaves as well as representative samples (same plant part, location and approximate stage of maturity) of *A. mexicana* leaves from the riverbed. Plant samples were shade dried and later analyzed by the Dairy One Forage Laboratory (complete assay methods of the laboratory are available at http://www.dairyone.com/Forage/Procedures/default.htm) for the following nutritional content: crude protein, acid detergent fiber, neutral detergent fiber, calcium, phosphorus, magnesium, potassium, and sodium. These macro- and micronutrients were chosen because they represent important feedants and antifeedants of the primate diet. High protein and low fiber can indicate a high-quality diet, and micronutrients are particularly important for gestating females. Data presented here are part of a larger project examining nutritional content of all food consumed during this period [LaFleur, 2008]. Our focus is to discuss the reliance on food consumed outside the forest, however, we present the nutritional content of all foods consumed during the study period.

Determination of Food Intake Rates and Time Spent Feeding

The number of minutes spent feeding was recorded for each focal animal. To determine food intake rate of the non-forest foods for each focal animal, the total number of leaves or bites of each food type was summed and divided by the number of minutes that individual spent feeding, to obtain an individual intake rate. Intake rate for the group was determined in the same manner, but by summing all leaves or bites of each non-forest food for the entire group, and dividing that by the total feeding minutes for the entire group. These percentages of time spent feeding, and time spent feeding on forest foods and non-forest foods for each group are presented for comparative purposes.

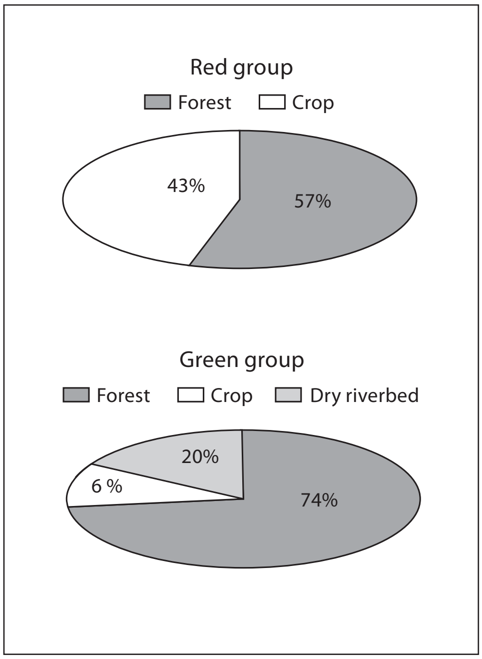

Fig. 2. Percent of time that each group spent feeding in the forest, in the cultivated crop (on sweet potato leaves and Mexican prickly poppy leaves), and in the dry riverbed (on Mexican prickly poppy leaves).

Data Analysis

To determine if there were significant differences in time spent feeding between groups, or if within group and sex differences occurred in intake rates between forested and non-forest habitats, non-parametric analysis of variance tests were used. The Mann-Whitney U test was employed when testing for differences between the two study groups and the Wilcoxon signed-rank test was used to examine if there was a within-group difference in the amount consumed in the forest versus outside the forest. Non-parametric tests were used because the sample sizes for each group were too small (RG = 3 adult females and 4 adult males, and GG = 6 adult females and 5 adult males) to test the assumptions of parametric statistical tests.

Results

Time Spent Feeding

RG spent 37% of its total observation time feeding, while GG, which had limited access to the crop, spent significantly more time feeding – 54% (Mann-Whitney U test, U = 8, p = 0.004).

RG did not feed in the dry riverbed, but spent 47% of its feeding time in the crop and 53% in the forest. GG spent 6% of its feeding time in the crop (used only when RG was not present), 17% in the dry riverbed, and 78% in the forest (fig. 2).

Table 1. Milligrams of crude protein, fiber (acid and neutral detergent fiber), calcium, phosphorus, magnesium, potassium, and sodium present in *L. catta* forest foods

	Plant part	CP	Fiber	Ca	P	Mg	K	Na
Acacia bellula	leaves	192	N/A	N/A	N/A	N/A	N/A	N/A
Ambirindola*	leaves	183	308	31.6	2.5	2.7	284	0.1
Amelo*	leaves	335	207	23.9	2.3	5.4	37.6	0.4
Azima tetracantha	leaves	168	377	77.7	1.8	3.3	12.6	0.08
Boerhavia diffusa	leaves	241	263	26.2	3	7.5	33.5	0.06
Bridelia pervileana	leaves	146	337	50.3	1.7	6.5	6.3	0.5
Byttneria voulili	leaves	221	361	27.4	1.9	4.8	15.5	0.04
Cenecio sp.	leaves	225	322.2	21.1	2.8	6	42	1.1
Combretum sp.	leaves	146	452	36.7	1.4	2.4	15.5	0.24
Dolichos lablalat	leaves	184	273	28.1	1.6	3.9	23.7	0.21
Enterospermum pruinosum	fruit	118	104.3	9	1.9	1.8	22.6	0.9
	leaves	140	650	23.3	1.3	2.7	20.4	0.05
Flacourtia ramoutchi	leaves	166	415	18.1	2.1	5.6	23.6	0.08
Gonocrypta grevei	leaves	114	383	36.5	1.5	3.1	23.5	0.1
Grewia sp. 1	leaves	129	434	15	1.4	3.8	13	0.07
Kijerandolo*	leaves	123	46.2	15.8	5.7	4.6	26.2	0.25
Kongo*	leaves	192	304	10.5	3.7	4.9	32.8	0.09
Lavaenafe*	leaves	225	32.2	21.1	2.8	6	42	1.1
Lobakanjirike*	leaves	292	29.6	33.7	2.9	5.9	40.5	0.34
Maerua filiformis	leaves	315	185	13.8	2.9	2.7	33.3	0.04
Metaporana parvifolia	leaves	187	383	26	2.4	3.9	40	0.15
Noronhia sp. 2	leaves	147	840	15.6	1.2	1.8	15.4	0.3
Plagioscyphys sp.	leaves	158	28.8	47.6	1.3	4.2	16.6	0.31
Quisivianthe pruinosum	flowers	231	N/A	N/A	N/A	N/A	N/A	N/A
Secamone sp.	leaves	174	30	37	1.3	4.7	19.7	0.44
Strychnos madagascariensis	leaves	168	549	57.3	0.9	8	11.9	0.29
Taboarandolo*	leaves, stems	269	298	44.5	3	8.3	21.9	0.24
Tamarindus indica	leaves	104	579	46.9	0.9	5.7	6.6	0.2
Temelapsis linearis	leaves	169	345	32.1	2	4.5	25	0.11
Tragia tiverneana	leaves	155	332	N/A	N/A	N/A	N/A	N/A
Tridax procumbens	flowers	163	83.8	10.2	5.1	2.9	25	0.13
Tridax procumbens	leaves	269	33.7	41.2	3	6.7	31.3	0.19
Vihipinde*	leaves	162	40.4	25.7	1.3	5.8	21.3	0.18
Vitex sp.	leaves	165	317	24.6	1.2	5.2	31.1	0.27
Xerophis sp.	leaves	114	341	21	1.5	6.6	27.6	0.2

* Indicates vernacular name, scientific name unknown.

Food Intake Rates: Forest Foods and Resources outside the Forest

A list of all foods consumed during the study period and the nutritional content of each food is found in table 1. Table 2 indicates the top five foods consumed by both groups and the percent of the top foods that each of the five food items represented.

Forty-three percent of RG's entire food intake (all foods) was comprised of the non-forest foods *A. mexicana* and *I. batatas* leaves, while just 12.8% of GG's entire

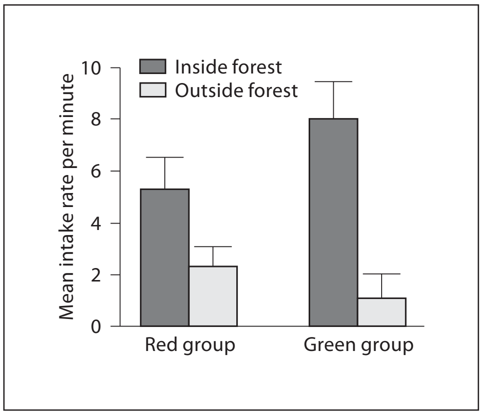

Fig. 3. Mean intake rate of food per minute (+SE) for each group when feeding inside and outside the forest.

Table 2. Top five foods of both groups during the study period

Top five foods	Intake rate per min	Percent of diet of top five foods
Green group		
Quisivianthe papionae flowers[1]	5.07	62.6
Ipomoea batatas bites/mouthful of large leaves	1.05	12.9 (35%)
Maerua filiformes mouthful of leaves	0.94	11.6
Argemone mexicana bites/mouthful of large leaves	0.52	6.4 (17.2%)
Secamone sp. leaves	0.51	6.3
Red group		
Quisivianthe papionae	3.17	54.4
Ipomoea batatas	1.54	26.4 (58%)
Argemone mexicana	0.7	12 (26.4%)
Secamone sp.	0.3	5
Metaporana parvifolia leaves	0.11	1.9

[1] The top ranked food (*Q. papionae* flowers) was available only for the last 5 days of the observation period. When removed from the analysis, the sweet potato leaves *(I. batatas)* and the Mexican prickly poppy *(A. mexicana)* make up a large part of the diet (shown in parentheses in column 3), particularly for RG.

diet was made up of these resources. While no significant difference was found in RG's mean intake rate between forest and non-forest foods (Wilcoxon signed-rank test, Z = –1.8, p = 0.06), GG's mean intake rate of foods inside the forest was significantly higher than outside (Wilcoxon signed-rank test, Z = –2.9, p = 0.003, fig. 3).

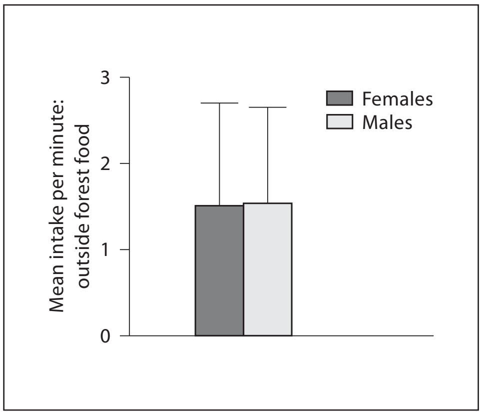

Fig. 4. Mean intake rate (+SE) of the fallback foods outside the forest (sweet potato leaves and Mexican prickly poppy leaves) by sex.

Table 3. Milligrams of crude protein (CP), fiber (acid and neutral detergent fiber), calcium, phosphorus, magnesium, potassium, and sodium present in 1 g of *A. mexicana* and *I. batatas*

Plant	Plant part	CP	Fiber	Ca	P	Mg	K	Na
A. mexicana	leaves, stems	295	306	14.5	3.4	3.8	40.3	0.2
I. batatas	leaves, stems	208	337	17.3	1.9	3.4	20.4	0.1

Non-Forest Fallback Food Nutrients

A. mexicana had higher percentages of crude protein and all minerals except calcium per gram dry weight when compared to *I. batatas* (table 3). Additionally, *A. mexicana* had lower fiber content when compared to *I. batatas*.

Male and Female Consumption of Fallback Foods

Females spent 42% of their focal time feeding, while males spent 49.5% of their focal time feeding. This difference in time spent feeding was not statistically significant (Mann-Whitney U test, U = 35, p = 0.37). Additionally, no significant differences were found in consumption rates of the non-forest fallback foods, even though the study occurred during late gestation period when pregnant females were coping with the dry season and effects of the cyclone (Mann-Whitney U test, U = 35, p = 0.66, fig. 4).

Discussion

Feeding during Non-Typical Seasons in Gallery Forest Habitat

Phenotypic plasticity is a potential mode for a taxon to colonize a broad ecological niche [Ménard, 2002]. The ability to exploit a wide variety of resources may be an evolutionary trait favored in unpredictable environments, such as those found in Madagascar [Wright, 1999]. Dietary plasticity, as found in *Lemur catta*, is suggested to be a key feature enabling the species to persist in the face of resource fluctuations due to natural disasters [Gould et al., 1999; Sauther et al., 1999]. The variation in ecological adaptability of *L. catta* may be exemplified through the wide range of habitat types in which it is found: spiny and gallery forests, scrub and brush land, anthropogenically induced savannah, and ericoid bush/subalpine habitat [Goodman and Langrand, 1996; Goodman and Rasolonandrasana, 2001; Sussman et al., 2003; Goodman et al., 2006; Gould, 2006], especially considering that *L. catta* is thought to have evolved in dry habitats of south and southwest Madagascar [Goodman et al., 2006]. Although its resource base is flexible, *L. catta* reproduction is highly tied to seasonal resources [Jolly, 1984; Sauther, 1992; Rasamimanana and Rafidinarivo, 1993; Sauther, 1993, 1998; Yamashita, 2002]. Females experience late gestation and early lactation periods during the driest parts of the year [Jolly, 1984; Sauther, 1994, 1998], and gallery forest populations normally depend on fruit and leaves of *T. indica,* as this species is a reliable source of protein and other essential nutrients [Sauther, 1992, 1994, 1998; Yamashita, 2002; Mertl-Millhollen et al., 2003]. In contrast to previous gallery forest studies, where tamarind made up 30–60% of the ring-tailed lemurs' diet [Sauther, 1992, 1993; Mertl-Milhollen et al., 2003; Soma, 2004; Koyama et al., 2006], the diet of the two *L. catta* groups in our study was comprised of <2% *T. indica*, as it was virtually unavailable as a result of the cyclone's devastation 7 months earlier. Although the two non-forest resources important to this study are often consumed by BMSR groups [Sauther, 1992; Gould et al., 1999; Gemmill and Gould, 2008], they were especially important during the period after the cyclone. Similarly, Soma [2004, 2006] found that species introduced to the Berenty Reserve reduced the effect of extreme food seasonality in gallery forest at that site, and Gould et al. [1999] noted that the introduced weed *A. mexicana* was an important *L. catta* food source during a drought at BMSR.

Many primate species (for example, savannah and anubis baboons [Forthman-Quick, 1986; Altmann and Muruthi, 1988; Strum and Manzolillo-Nightingale, 2006], rhesus macaques [Malik and Southwick, 1988], Japanese macaques [Watanabe and Moroyama, 2005; Agetsuma, 2007], and brown capuchins [Galetti and Pedroni, 1994]) include invasive or agricultural plants in their diets, either because their natural foods are insufficient, or because they have a preference (i.e. taste or ease of processing, for example) for cultigens. Primates who crop raid experience an immediate increase in foraging efficiency [Brennan et al., 1985; Fa, 1986; Forthman-Quick, 1986; Altmann and Muruthi, 1988], and crop foods tend to be higher in energy per food unit, densely spaced, and easy to exploit, enabling crop raiders to meet their metabolic needs sooner [Saj et al., 1999].

Comparative ease of processing is most likely why RG vigorously defended the sweet potato leaves and spent nearly half of its feeding time consuming these leaves instead of focusing on *A. mexicana*, which was also highly abundant and higher in measured nutrients. It is also possible that the sweet potato leaves tasted better, as they are a human cultigen and thus not likely to contain as many secondary compounds as wild plant foods. Conversely, the extensive processing time required for *A. mexicana* is most likely why GG spent far more time feeding in the forest. This plant is covered in sharp thorns, and the lemurs must remove the leaves from the plant one at a time, hold the stem and chew from the base up in order not to puncture

Fig. 5. Ring-tailed lemur consuming the thorny but important fallback food *A. mexicana*.

their mouth [Gemmill and Gould, 2008; LaFleur, 2008] (fig. 5). Cultigens may be considered to have higher nutritional value when compared to weed species or other non-cultigens, however, as demonstrated here, weed species can be as or even more nutritious than cultigens, but may require increased processing time.

Lack of Sex Differences in Consumption of Fallback Foods

Although this study was conducted during the late gestation period when female nutritional needs are high, we found no sex difference in consumption of these fallback foods, despite their nutritional value or ease of procurement. Behavioral differences were evident when groups fed on *Argemone* and *Ipomoea*, in that males would often stay a few feet behind females, and wait to eat until females dropped or discarded plant parts. However, these behavioral differences did not significantly affect amount consumed or rates of consumption, which is contrary to predictions based on need of reproductive females. Females experience late gestation during the driest parts of the year [Sauther, 1994, 1998] and normally depend on the crucially important fallback resource *T. indica,* as it is a reliable source of protein and other essential nutrients [Sauther, 1992, 1994, 1998; Mertl-Millhollen et al., 2003; Sauther and Cuozzo, in press]. Sauther [1994] found that pregnant females at BMSR fed more on flowers and fruits than did males, and males focused more on leaves. However, since our study took place in a year of natural disaster, when little to no fruit was available, it was not possible for females to focus on such resources at this time. Sex differences in feeding behavior and consumption were not observed in the consumption of strict forest foods during this study either [LaFleur, 2008], nor were sex differences in any feeding or nutrient variable found in a study of reproductive *L. catta* females residing in a spiny forest habitat at a different site (Berenty Private Reserve), where tamarind was rarely available and lemurs had to leave their home range to consume it [Gould, in prep.]. Thus, it is possible that sex differences in feeding in *L. catta* may only arise in relation to consumption of preferred foods in gallery forest habitat during a year when tamarind and flower resources are readily available, and not during years when natural disasters have affected the resource base, or in habitats that differ markedly from that of a gallery forest. Furthermore, the two fallback foods considered in our paper are distributed very widely in large patches, where the entire group can spread out, and this may have mitigated sex differences in feeding since the resources were plentiful.

Feeding outside the Forest: Costs, Benefits, and Risks

Primates foraging outside their forest habitat are subject to higher injury or predation risk by humans, non-human predators, and conspecifics [Strum, 1987; Else, 1991; Saj et al., 2001]. Human-lemur conflict at BMSR is lower than expected, when compared to other crop-raiding primates [Strum, 1987; Saj et al., 2001]. Loudon et al. [2006, p 65] conducted interviews with 12 men who live in the vicinity of BMSR, and noted that *L. catta* 'enjoy a culturally protected status' which results from 'fady' or traditional taboo against harming lemurs. This taboo may help explain why the land owner in this study did not try to harm the crop-raiding lemurs, even though they spent significant amounts of time depleting his crop resource. It is important to note that this interpretation is based on a single agricultural field with a single owner, and although we believe his actions (allowing lemurs to consume crop foods without threat) and opinion genuine (he or his family were not compensated and do not work for the Reserve) and similar to those of other owners of neighboring agricultural plots, this may not entirely be the case.

At BMSR ring-tailed lemurs which leave the forest are subject to increased predation pressure, particularly from feral dogs and cats and predatory birds [Sauther, 2002; Gould, pers. obs.]. However, since humans in the Beza Mahafaly area do not generally harm crop-raiding lemurs, human presence may actually offset the risk of predation for these lemurs when they are foraging in the crop, as they may deter aerial and terrestrial predators. Another risk for these groups includes territorial altercations associated with defending or accessing the crop foods. Even though RG (n = 7) was smaller than GG (n = 11), it defended the crop territory vigorously and engaged in daily altercations to maintain this territory. Similarly, GG repeatedly attempted to access crop foods, despite having to fight and only being successful when RG was not present. Although associated with an increased risk, foraging outside the forest (especially on crop foods) can be calorically rewarding, and was an important aspect of ring-tailed lemur diet in this study. This study further emphasizes the ecological and dietary flexibility of this lemur, which has been characterized previously as a highly adaptable 'edge' or 'weed' species [Sussman, 1977; Gould et al., 1999; Sauther et al., 1999; Gould et al., 2003].

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